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### THE NORTHERN FLINT CORNS

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The slender-eared, wide-kernelled flint corns of New York State and New England were for centuries (see Table III) the commonest type of maize in eastern North America. As dent varieties pushed northward and as earlier and earlier varieties of dents have been developed, these wide-seeded flints have been restrictéd to an ever-narrowing fringe along the northern edge of maize cultivation. Today they are of secondary economic importance but their role in the production of the very varieties which supplanted them makes their study imperative to the modern corn-breeder. In addition to their intrinsic interest as a well-marked and formerly widespread type of Zea Mays, their close identification with the Indians of the eastern United States renders their history and relationships of compelling interest to the American archaeologist.

During 1944-46 a collection of these northern flint varieties was brought together and grown in the experimental plots of the Pioneer Hi-Bred Corn Company, at Johnston, Iowa. We are especially indebted to Dr. R. G. Wiggans of Cornell University for suggesting sources of seed for a number of eastern varieties.

Tables I and II list the varieties by name, in so far as this was known, and their places of origin. A photographic record was made of one plant of each collection, and herbarium specimens were prepared of two or more tassels (male inflorescence). Internode diagrams (Anderson and Schregardus, '44) were made of representative plants, and the following record was made of the tassels: tassel branch number, condensation index (Anderson, '44), number of tertiary branches, presence of whorling in the central spike, and number of paired spikelets per whorl. Open-pollinated ears were obtained from each culture and were scored for cob and kernel color, kernel width, kernel thickness, amount of denting, and diameter of the shank below the ear. These various scores and measurements are presented in Tables I and II.

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For cytological study, sporocytes from each of the varieties were killed and fixed in 3 parts alcohol to 1 part propionic acid. After 24 hours at room temperature they were stored in a refrigerator until they were smeared in propionic carmine. Chromosome knob numbers were obtained from each culture. The results are tabulated in Tables I and II and are discussed in detail below.

#### MORPHOLOGY

It was immediately apparent that, in spite of much plant-to-plant variation, the northern flints were essentially homogeneous at the eastern end of their range in New York and New England but became increasingly variable as the Great Plains were approached. This is equally true whether one considers the morphology of the plants, the appearance of the ears, or the knob numbers of the chromosomes. This is also true of the extensive archaeological material which has been examined and which is described later in this report. The following description therefore applies to the relatively uniform material from the Northeast. As shown in Table II, similar varieties are also found in the northern Great Plains but there they are accompanied by other kinds of flint corns (pls. 3 and 4).

The ears of the northeastern flints are characteristically long and slender with 8 to 10 rows of wide, crescent-shaped kernels (pls. 1, 2). The cob is strong and proportionately large, particularly toward the base, and the shank or ear-stalk is thick and well-developed. Frequently the base is noticeably larger than the rest of the ear, and even in those varieties which do not exhibit this character in a prominent fashion, a tendency in this direction may be seen in increased row numbers, irregular kernels, or irregular rowing at the base of the ear. This increased basal development in the northeastern flints is most conspicuous when comparisons are made with 8-rowed varieties from western Mexico and with some of the flints of the southwestern United States. Such varieties taper toward the base instead of becoming increasingly wider. As might be expected, the northeastern flints are of early maturity. They have more suckers or tillers than the common dent varieties from the same area, and these tillers are usually shorter than the main stalk and often bear malformed ears and tassels. Prop-roots are less common than in United States dent varieties; there are usually very few above the level of the soil surface. The culms are small and slender with long internodes and are lighter green than most dent varieties. The leaves are narrow and the ears are borne on long shanks. The leaves of the ear shoot (the husks) have conspicuous blades (fig. 4) which are sometimes referred to as "flag-leaves" by sweet-corn breeders. The combination of slender culms, irregular tillers, and well-developed flag leaves gives all these flints a

distinctive general aspect.

The tassels of the northeastern flints are wiry and open. Tassel branch numbers are mostly from 12 to 16. There is little or no condensation (fig. 2), and the spikelet pairs are thinly and evenly spaced along the secondary branches. The tassels have a slender axis with long internodes. The central spike is thin and

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Fig. 1. Actual diagram showing branching pattern and spikelet arrangement of a typical tassel of Longfellow Flint. Left: the 11 nodes of the branched portion of the tassel, showing the number of branches at each node (in this case 1 or 2) and the approximate direction in which they pointed. Immediately above these 11 nodes are the first 5 nodes of the central spike, each of which bore 2 pairs of spikelets. Right: a diagram to scale of the actual position of all the spikelets on an 8-cm. section of the central spike. The technique is adapted from that used by Mangelsdorf ('45) and represents a portion of the spike as if it had been slit down one side and flattened out from a cylinder to a rectangle. Scale at left in cm. All the spikelets in this specimen were in pairs, one member of each pair being sessile and one pedicellate. All were in 4 ranks and, aside from 1 extra pair at the lower right-hand corner, were arranged 2 pairs to a node, the pairs being at right angles to the next nodes above or below; in other words, decussate, which means that if there were spikelet pairs at the north and south ends of a particular node, those at the next node would be on the east and west sides, those at the second node at the north and south again, etc.

without the conspicuously thickened central portion so characteristic of most dent corns and certain varieties of popcorn. The arrangement of the tassel branches is more regular than appears from casual observation. In those varieties which are mostly 8-rowed it is as follows: The upper two branches are opposite and below



SUCCESSIVE SECONDARY BRANCHES FROM BASE TO APEX

Fig. 2. Lengths of tassel branches, condensation index (C. I.), and number of tertiary branches for typical individuals of six varieties of northern flint. (See Anderson, '44 for details of scoring.)

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them is a series of branch pairs which are opposite or practically so. Toward the base of the tassel these pairs become increasingly indistinct until finally there is a single branch at each node. The lower two branches are usually 2-ranked and on opposite sides of the axis though well separated. There is a strong tendency for the tassel branches, as a whole, to be quite regularly 6-ranked but aside from this we have been able to find no general regularity in the way they are arranged on the stem, which varies between the clearly opposite pair just below the central spike and the alternately 2-ranked pair at the base of the tassel. Detailed records

of a typical tassel are presented in fig. 1.



#### Chromosome knob number

Fig. 3. Frequency distribution of chromosome knob numbers in dent corn inbreds.

The arrangement of the central spike is surprisingly simple and does not seem to have been previously described. In the 8-rowed crescent-seeded flints it is clearly whorled. At each node there are two pairs of spikelets, one of each pair being pedicellate and one sessile. The pairs at each node are at right angles to those immediately below and immediately above, so that the spike, as a whole, is 4-ranked and decussate. This simple arrangement is somewhat masked by a slight twisting of the axis, and in some plants by a low degree of multiplication (Cutler, '46, p. 269). In 10- and 12-rowed varieties the patterns may be modified in various ways. If there is enough condensation (Anderson, '44) to telescope some of the nodes on the secondary branches, there may be additional spikelets at the nodes, or the clear division into nodes may not be apparent and the spike will seem to be arranged spirally instead of being whorled. In some of the Plains flints with 12-rowed ears the central spikes may be whorled but the whorls have three spikelet pairs instead of two as in the 8-rowed varieties.

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Variety	Source	Cob color	Kernel color	Kernel thickness (cm.)	Kernel width (cm.)	Dent- ing*	Diam. shank (cm.)	Number of rows	Number of chromosome knobs**
Canada Flint	Feeding Hills, Mass.	White	Yellow, purple	.46	1.0	0	1,4	8	0
Dutton	Newark Valley, N.Y.	White	Yellow, purple	.40	1.0	0	2.1	80	2
Harris Mammoth Yellow	Rochester, N.Y.	White	Yellow	.44	1.1	0	1.6	~	0
Longfellow	Ontario	White	Yellow	.41	1.0	0	1.5	80	1
Mammoth Yellow	Ithaca, N. Y.	White	Yellow	.38	1.0	0-1	1.6	00	. 2
Parker's Flint	Potsdam, N. Y.	White	Purple, red, yellow	.44	1.0	0	1.1	8	0
Quebec Flint	Restigouche, Que.	White	Yellow	.20	.5	0	8.	8-10	1
Smut Nose	Bath, N. Y.	White	Yellow, red	.48	1.0	0	1.7	~	2
Stevens	Ithaca, N. Y.	White	Yellow, red	.41	1.1	0	2.4	80	0
Thayer Flint	Searsport, Me.	White	Yellow	.44	1.0	0	1.9	80	0
Thompson Flint	East Andover, N. H.	White	Yellow, red	.45	1.0	0	1.4	80	0
12-row Red Flint	Dryden, N. Y.	White	Yellow, red	.40	6.	0	2.1	12	1
12-row Yellow Flint	Dryden, N. Y.	White	Yellow, red	.44	∞.	0	1.6	12	0
Wilbur's Flint	Hudson Falls, N.Y.	White	Yellow	.50	1.0	0	1.4	8	0

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	Source	Cob color	Kernel color	Kernel thickness (cm.)	Kernel width (cm.)	Dent- ing*	Diam. shank (cm.)	Number of rows	Number of chromosome knobs***
	North Dakota	White	Yellow, white,						
	North Dakora	White	Yellow, white,	++.	1.0	0	2.1	8-12	1
	North Dakota	White	Yellow, white,	.44	6.	1-0	1.2	8	
	North Dakota	White	Yellow, white,	.46	6.	0-1	1.9	10	1
4	South Dakota	White	Yellow, white,	.42	6.	1	2.1	8-10	0
			purple, red	.46	6.	0	2.3	14	0
	North Dakota	White	Purple, yellow	.40	.8	0-1	1.9	8-12	0
allow	Town	White	Yellow	.44	2.	0	1.9	12	2
MOTO	Madison. Wis.	White	Yellow minulo	10.	1.0	0	1.6	8	0
	North Dakota	White	Red Red	143	1.0		1.1	01-8	1
t	North Dakota	White	Yellow, purple	.42	. 8.	0	2.1	8-10-12	~ ~
	North Dakota	White	Yellow, purple	.42	.8	0-1	1.5	12 12	
	North Dakota	White	Yellow	.36	.6	0	1.2	8-12	2
	Wisconsin	White	Yellow	.44	.7	1-0	6.	12	2
	Iowa	White	Yellow, purple	.40	.6	0	1.5	12	
	Tama, Iowa	White	White, purple	.40	6.	0	2.2	00	1
	North Dakota	White	Yellow, purple,						
			white	.42	6.	0	1.9	12	0
	Madison, Wis.	White	Yellow, red,						
			purple	.50	6.	0	1.6	8	1
	Ames, Iowa	White	Yellow, white	.42	.7	0	1.1	8	0
	South Dakota	White	Yellow, white,						
			purple, red	.47	6.	0	2.1	12	3
	North Dakota	White	Purple, yellow	.40	1.0	0	1.8	8	1
	North Dakota	White	Purple, yellow,						
			White	.44	1.0	2	11	17	2

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soft starch; 1-visible soft starch; 2-slight der ontaminated with northern flint varieties. organizer knob on chromosome 6. visible U probably nclu OL not enting I but r but do 1

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	Variety	Argentine Flint**	Assiniboine	Dakota Squaw	Dakota White	14-row Dakota Flint	Gehu Gehu Harris Mammoth Ye	Mandan & Arikara Mercer County Flint	Rainbow Russian Extra Early Russian Extra Early	Russian Extra Early Jac & Fox Jantee	Smut Nose	panish Pop 2-row Dakota Flint	Winnebago Zuni Blue	* 0-no der ** So called *** Numbers
1		A	A	D	D	14	OGH.	NW	RuRu	Ru Sai	Sm	Spi 12	Zu	1

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MUSEUMS VARIOUS IN MAIZE PROTOHISTORIC H TABLE OR PREHISTORIC OF ECTIONS

				Num	ber of	rows				Ker	nel wid	lth in n	nm.		
State	Site	Museum	8	10	12	14	16	9	2	8	6	10	11	12	-
New York	Alhart, Monroe Co.	R**								1	1			2	
New York New York	Sackett Co. Kahler, Livingston Co.	K	20	2								-			
New York	Castle Creek, Broome Co.	R									1	3	-		
New York Ohio	Silver Wheels Kettle Hill, Lancaster Co.	HO	1 60	14	3							-	-		
Ohio	Canter's Cave	0		1	2	3									
Ohio Ohio	Gartner Village Baldwin Village, Lancaster Co.	0 & M							-	~	1	I	1		
Ohio	Fuert	W	3	4	2										
oido	Baum Madisonville (Mound)	M&F N	4 5		1				1	24	3	4	3		
Michigan	Gibralter, Wayne Co.	M	2												
Illinois Illinois Kentucky Tennessee Tennessee Tennessee S. Carolina Georgia Alabama	Kincaid (near Ohio R.) Cable Site Fisher Fisher Kings Mound (Wickliffe) Norris Basin 2322 Norris Basin 2347 Norris Basin 2247 Norris Basin 2215 McDowell Mound, Kershaw Co. Stallings Mound, Columbia Co. Stallings Mound, Columbia Co.	XXXXXXXXX	13 6 1	1 1 1 1 4 1	2 3	2			6 1	1 2 1 2	m	7			

SUMM

StateStateStateIowaNear GlenwoodAS. DakotaRygh SiteMS. DakotaLeavenworthMS. DakotaElk CreekMNebraskaPonca FortMNebraskaHill SiteM		8 1	1	2	14	16	9	7	8	6	10	11	12	13	Kemarks
IowaNear GlenwoodAS. DakotaRygh SiteMS. DakotaLeavenworthMS. DakotaElk CreekMNebraskaPonca FortMNebraskaHill SiteM													**	-	
S. Dakota Leavenworth M M M M M M M M M M M M M M M M M M M		-			5							-			No denting Ear elliptical,
Nebraska Ponca Fort M Nebraska Hill Site M M	4	= -													Historic Arikara.
AT LA	A	1									-	-			Strong row pairing Strong row pairing
INEDFASKA INCAT LYNCH, BOYD CO. M.		2										4	-		Ear widest above base.
Kansas Tobias Site, Rice Co. Kansas Doniphan Site, Doniphan Co. N		0.0			1			1	8	1					Late prehistoric Mid 16th century Post European; mid 18th century
Kansas Fanning Site Missouri Steed-Kiska, Platte Co. N		- 0		~							1				No row pairing. Ear
Missouri Jane, McDonald Co.		1			***					1	4				from a cache pit Smooth dimpled dent. White bluff rock shelter
Arkansas From caves in N. W. Arkansas M Arkansas From caves in N. W. Arkansas A				*		1		1							No row pairing No denting

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The northeastern flints make excellent cytological material; as compared to most other United States varieties they are easy to smear and yield a high percentage of good preparations. This is, in part at least, the result of their being knobless or essentially so, that being the outstanding cytological feature of these corns. A summary of chromosome knob numbers for flints from the Northeast and from the Northern Plains is presented in Tables I and II. It will be seen that, aside from the organizer knob on chromosome 6, the northeastern flints are knobless or have only one or two knobs. The organizer knob is never large as in some Central American varieties. On the contrary, it is usually extremely small, lightstaining and inconspicuous (fig. 5). The knob positions in the northern flints are also characteristic, as had previously been reported by Longley ('38) for the varieties of the northern Indians. When knobs are present in these varieties they are usually either small and terminal on chromosome 9 or two small knobs on the long arm of chromosome 6. The form of the terminal knob on chromosome 9 is also characteristic. It may be more or less cleft at the apex, or it may taper to an acuminate point; it is never large and cylindrical as in certain varieties from western Mexico. In all cases knobs in the northern flints are small; often they are only slightly larger than a large chromomere.

Since the varieties included in this study were from open-pollinated seed and were more or less heterozygous one might expect knob numbers to vary considerably within varieties. Actually the variation is slight, usually not more than one knob. Where different knob numbers were observed the number listed represents the average of a number of counts. Among the varieties examined cytologically, two (Parker's Flint and Twelve-row Dakota) were found to contain, in addition to the normal chromosome complement, one and two pairs of B chromosomes. The B chromosomes in the variety "Twelve-row Dakota" were unusually large and the pairs were frequently joined at pachytene of meiosis.

#### ARCHAEOLOGY

The rapid advances of American archaeology in the last few decades have added greatly to our knowledge of the history and development of maize. As additional collections of prehistoric material become available and as cultural sequences are more accurately determined, the history of corn in North America will no longer be a matter for argument. It will instead come within the domain of measurement as various collections are recorded and carefully compared with one another. For the northern flint corns, while some details remain to be filled in, the outlines of the story are already clear. They are shown in map 1 and a detailed report is presented in Table III. Before going into the minutiae of these collections, the nonarchaeological reader may be helped if we anticipate the chief conclusions: Eight-rowed flints, similar to those described above, were widespread in pre-Columbian times in the eastern United States. They go back to approximately 1000 A. D., and over wide areas in the *eastern* United States no other kind of

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Fig. 4. A single ear of Stevens' Flint showing extensive husk-leaf development representative of many varieties of northern flint corn.

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Fig. 5. Pachytene chromosomes of Longfellow Flint showing small organizer knob on chromosome 6. The largest arrow points directly to the organizer knob. It will be noted that the knob is so small as to be scarcely visible against the side of the nucleolus and is only slightly larger than the terminal chromomere of the satellite just below it. The smaller arrow points to the small terminal knob on chromosome 9.





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Map 1. Distribution of collections of prehistoric corn in the eastern United States: large dots, crescent-seeded 8-10 rowed flints (i. e., like northeastern flints); small dots, various other types.

maize has been reported in archaeological remains. In the Great Plains, by contrast, there were widely divergent types of corn as well as northern flints and apparent mixtures with them. The sequence of these types of flint in the Great Plains remains to be worked out. The situation in the American Southwest is equally complex but one fact is certain: The northern flints arrived there relatively late (about 1300 A. D.), long after other types of maize had been established in that region. The facts on which these conclusions are based are presented in condensed form in Table III and map 1. These summarize the collections of archaeological maize from the Great Plains and the eastern United States which we have so far examined, some 36 in all. They represent all the collections readily available at the Rochester Museum, the Peabody Museum of Harvard University, the Ohio State Museum at Columbus, the Museum of Ethnobotany of the University of Michigan, the National Museum at Washington, the Library of the Iowa State College at Ames, and the Chicago Museum of Natural History. To the curators and staffs of these museums we are greatly indebted. They not only made the material available for study but supplied us with literature and references in addition to much general information on archaeological matters. It will be noted that nothing from the southwestern states is included in this survey. The situation there is much too complex for discussion here and is somewhat outside the scope of this paper. For a detailed report on one prehistoric collection of southwestern maize

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which includes 8-rowed flints, see Anderson's appendix to Haury's ('45) report on Painted Cave. For a general discussion of the evidence on types of maize in the Southwest see the fourth chapter, pp. 39-55, of Carter's ('45) "Plant Geography and Culture History in the American Southwest."

Some of the data in Table III are summarized in map 1. At least three main types of corn occur in the Northern Great Plains: (1) Varieties very similar, if not identical, to the northeastern flints described above. They have wide, crescentshaped seeds, thicker at the apex of the kernel than near the germ. They are straight-rowed with strongly paired rows, and are predominantly 8-rowed. (2) In the Northern Great Plains, in addition to the above varieties, are others which are more or less similar but have higher row numbers and smaller, squarer kernels. (3) From rock shelters and caves from the Ozarks to southern Ohio are found collections of a very different type of corn. Some of these are well preserved. From others the evidence is fragmentary. They resemble the so-called prehistoric Basketmaker corn of the Southwest in their irregular-shaped kernels, their ears, which taper to the base as well as to the tip, and their high percentage of ears with row numbers from 12 to 14. Their presence in this area and their resemblance to Basketmaker corn raise questions which are completely outside the scope of this paper. The point in question is the 8-rowed crescent-seeded flints. Map 1 and Table III demonstrate that such varieties have been in the eastern and northern states for some centuries at least and that they were once very widespread there.

If we catalogue the varieties of corn by their general resemblance to each other in all characters rather than by the texture of their endosperm (Anderson and Cutler, '42) it will be seen that a number of sweet corns, a few of the older varieties of popcorns, and some of the flour corns of the eastern Indians are very closely related to the northeastern flints. They resemble them in their early maturity, crescent seeds, predominance of 8 rows, tillering, flag leaves on the ear, absence of prop-roots, and structure of the tassel. The few which we have examined are also very similar cytologically.

#### DISCUSSION

The northern flints as ancestors of modern corn-belt varieties.-

While the northern flints, as such, are now little more than a curiosity in much of the region where they were formerly grown, they are indirectly of both practical and theoretical significance because they are at least one of the ancestral types of the varieties which replaced them. There is abundant evidence that the varieties of the United States corn belt originated by repeated hybridization between the northern flints and soft-textured southern dents.

Until the early 1800's nothing like the big cylindrical, yellow maize of the corn belt, with its keystone-shaped, dented kernel, was known in the United States or elsewhere. As American agriculture developed and pushed westward the northern flints were progressively more and more mixed with soft white dents spreading up from the South. The latter were in many ways similar to some present-day Mexican varieties. Lorain, whose book appeared posthumously in

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1825, described the ears of these southern dents as "not very long, neither is the cob so thick as that of the big white and yellow [flint]. But the formation of the grain makes the ears very thick. They frequently produce from thirty to thirtytwo and sometimes thirty-six rows of very long narrow grains of a soft, open texture. These grains are almost flat, at their outside ends." He also states that this dent "ripens later than any other but is by far the most productive." (p. 203). The commonest name for these soft dents was "Gourdseed", since the flat kernels with a collapsed and more or less pointed tip resembled a pumpkin seed or gourd

seed.

Lorain discussed in detail the results to be obtained from mixing Gourdseeds and flints and went on to say:

"The quantity of the Gourdseed corn mixed with the flinty yellow corns, may be determined, so as to answer the farmer's purpose. When the proportion of the former greatly predominates, the grains are pale, very long and narrow, and the outside ends of them are so flat that but little of the indenture is seen. As the proportion of Gourdseed decreases in the mixture, the grains shorten and become wider, and their outside ends grow thicker. The indentures also become larger and rounder, until the harder corns get the ascendancy. After this the outside ends of the grains become thicker and more circular. They also grow wider, and the fluted appearance between the rows increases. The indentures also decrease in size until they disappear, and the yellow flinty varieties are formed. But as I believe, not so fully but that the latent remains of mixture will forever subject it to more or less change." (loc. cit., pp. 205-206).

The churning and rechurning of the Gourdseeds and the flints continued for several decades. By 1837, P. A. Brown listed seven different varieties known to him which had originated in that fashion. For the year 1850 we have an unusually complete picture. Before there was a Federal Department of Agriculture, the Patent Office published an annual summary of the progress of American agriculture; questionnaires were sent out to leading farmers and the replies were summarized and woven into an essay. For 1850 (U. S. Comm. Patents Rept., '50) the replies were printed practically as written, not even being sorted according to states. Since the first question to be answered had been: "What varieties of corn are most esteemed in your vicinity?", the replies give a detailed picture of the kinds of corn grown in the United States in the middle of the 19th century. The corn belt was just then taking shape in Ohio. Three of the replies from that state describe the mixing of flints and Gourdseeds which was taking place. "We cultivate several varieties of what is here called gourd-seed. They are all nearly a hybrid between the rough gourd-seed of the South and the flints of the North." (p. 371). Another letter asserts that the best varieties are "obtained by mixing the large Southern corn with that of the North." (p. 396). Another states that there are "many good varieties, mostly crosses between gourd-seed and the small flint." (p. 454). Only one reply about corn was received from Illinois which was then outside the corn belt (p. 245). It reports that in the vicinity of Quincy the most esteemed variety is "a species obtained by mixing the large yellow corn of Kentucky with the yellow flint." The white Gourdseed is also said to be planted. Mixtures of Gourdseed with various southern corns are specifically mentioned in reports from North and South Carolina, Virginia, Alabama, and Mississippi.

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Northern flints alone are mentioned for Maine, New Hampshire, Connecticut and New York, and they were still among the outstanding varieties for Massachusetts, Ohio, Kentucky, Illinois and Michigan. The expression "dent corn", incidentally, is used only in the three letters from Michigan (pp. 309, 410, 412).

There can be little doubt then that our corn-belt dents originated during the first half of the nineteenth century by a manifold mixing of northern 8- and 10rowed flints with many-rowed southern dents. In addition to the precise evidence given by Lorain and the Patent Office report for 1850 there are numerous references and descriptions in other agricultural writings. For detailed accounts the reader is referred to Edward Enfield's monograph on "Indian Corn," published in 1866; Fearing Burr Jr.'s, "Field and Garden Vegetables of America," 1863; Browne's, "Essay on Indian Corn" in The 'Farmers' Cabinet' for 1838, and the 'Transactions of the New York State Agricultural Society' for 1848.

### The importance of northern flints in modern corn breeding.-

The demonstration that our corn-belt dents are derived in part from the northern flint corns is of more than academic interest. It has been shown (Anderson, '39) that in crosses where any considerable number of genes are concerned the total forces of varietal cohesion are vastly greater than is usually appreciated. In such crosses all the multiple-factor characters will be partially linked with one another, and while a bewildering variety of new forms may appear, on the whole, the combinations of characters which went into the cross together will tend very strongly to stay together in the hybrids. If the number of segregating genes exceeds three per average cross-over segment (a not unlikely figure in crosses between northern flints and southern dents) then the linkages can be broken only by long generations of controlled breeding. Though approximately a century has elapsed since the mixture of the southern dents and the northern flints was begun, we may well expect that enough of the genes contributed by the flint varieties are still so linked with one another, on the average, to render this linkage worthy of consideration in any corn-breeding program. In producing hybrid corn, for instance, some of the difficulties encountered are due to the fact that we are not working with a homogeneous mixture of dent corns as such; we are working with a mixture containing large blocks of germ-plasm of southern dents and of northern flints. Hard kernels, a low row number, cylindrical ears, and early maturity were qualities which went into corn-belt corn from the flints. It is a matter of common knowledge among experienced present-day corn breeders that these qualities still tend to stay together. Knowing that these qualities went in together from the flints, it should not take too long, by experimental breeding, to produce at least a rough estimate of their distribution in the germ-plasm of corn-belt varieties. Are they scattered equally over all ten chromosomes, or are they concentrated on a few? Are the gene differences to be estimated in the tens, the hundreds, or the thousands? It should be possible within a reasonable length of time to answer these questions in at least a provisional way, and data of this nature should be quite

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useful to the modern corn breeder in his efforts to improve existing inbred lines and to create new and better ones.

Relationship between chromosome knob numbers and morphology of inbreds.-

There is as yet little exact evidence as to how completely the gene combinations introduced from the northern flints have been broken up in modern dent corns. Our determinations of chromosome knob numbers in 65 inbred lines of corn-belt maize bear directly on this point (fig. 3).

While the numbers of inbreds investigated is still too small to represent an unequivocal demonstration, the general trend in ear and plant morphology from one extreme to the other as one passes from inbreds with low knob numbers to those with higher numbers is most suggestive. The inbreds with knob numbers of approximately two are clearly the most like the northern flints of any of the 65 which have been studied. It would seem that the total effect of the forces holding the germ-plasm of the northern flints together is so strong in modern maize, even after a century of mixing, that the coherence can be demonstrated cytologically. If this be true, it represents racial coherence of a very high order of magnitude, for the knobs serve as cytological markers for only a portion of the germ-plasm. Any specific knob can serve only as a marker for the arm or part of arm of the particular chromosome in which it occurs. Since there are 10 chromosomes and therefore 20 chromosome arms, the difference between the high knob lines of 8 and the low knob lines of 2 is at most a difference in only 6 out of the 20 arms, or 30 per cent. It seems, therefore, significant that with markers in only 30 per

cent of the chromosome arms, there is still an indication of resemblance to the northern flints in the low knob inbreds.

It may be that when a larger number of inbreds have been examined the relationship between low knob numbers and flint-like characters will not be as definite as these preliminary results have indicated. The low knob number of the northern flints, however, is definitely established. This fact poses a number of questions since it seems to be in direct opposition to Mangelsdorf and Cameron's ('42) pioneer work on the same subject.

Mangelsdorf and Cameron determined the knob numbers of over 150 varieties of maize from Guatemala and demonstrated the association of high and of low numbers with various contrasting characters of the ear and plant. Two of the most definite associations which they established were between high knob number and cylindrical vs. tapered ears, and with straight rows vs. irregular rowing. On the basis of their findings we might expect the northern flints to have the highest knob numbers of any United States varieties of corn. Actually they have the lowest, as we have shown above. These two facts, however, are not as diametrically opposed as they might seem. The corn of the United States is not the corn of Guatemala, nor could all of it have been directly derived therefrom. Much of it, theoretically the greater part of it, must have spread into the United States by way of Mexico. For that country we have only about 50 knob determinations but in

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general they agree with those of Mangelsdorf and Cameron. In western Mexico there is a whole group of varieties with cylindrical ears, high-lodging resistance, and growing chiefly at low altitudes. They have high knob numbers as Mangelsdorf and Cameron would predict. In Central Mexico, mostly at very high altitudes, there is a group of tapering-eared dent corns which lodge badly and are smut-susceptible. Mangelsdorf and Cameron would predict them to have generally low knob numbers which they do, being from 0 to 5 in the material we have investigated. Much of the dent corn of Mexico is intermediate between these two extreme types (Anderson, '46), and the few examples we have investigated have intermediate knob numbers as might be expected. It was such varieties as these which eventually spread northward into the United States. If for the moment we sidestep the question of where the northern flints came from originally but keep in mind that they have few or no knobs, then our results come closer to falling into line with those of Mangelsdorf and Cameron. By a mixture of old, southern dents with mediumly high knob numbers and northern flints with few knobs or none, then a situation such as we have described would have developed.

### Origin of the northern flints.-

The above hypothesis is satisfactory as far as it goes, but it leaves unexplained the origin of the northern flints and advances no reasons for their having few or no knobs. Only the most tentative of explanations can be offered at the present time. As has been pointed out above, the northern flints are characterized by wide, crescent-shaped seeds on a cylindrical, few-rowed ear with a strong cob more or less enlarged at the base and borne on a stout shank. This is a distinctive combination of characters. Since somewhat similar varieties are known in the American Southwest, Mangelsdorf and Reeves originally suggested ('39) that the northern flints spread into the eastern United States from that direction. In this respect they are almost certainly wrong. We have specific archaeological evidence that the northern flints are definitely pre-Iroquoian in eastern North America (see pl. 6). There is abundant and definite evidence (Carter, '45; Carter and Anderson, '45) that varieties like the northern flints did not reach the American Southwest until after 1200 A. D. There is even some evidence to suggest that they reached the Southwest as varieties relatively similar to those in the East and that they then underwent hybridization with some of the varieties already present in the Southwest to produce the typical long-eared sorts of the modern pueblos (Haury, '45). Furthermore, the very similar long-eared varieties of northern Chihuahua most certainly represent relatively late southern extension into Mexico

as had already been determined from cultural evidence (Sayles, '36).

If the northern flints could not have spread from the Southwest, whence could they have come? Varieties with wide kernels, stout cobs, and a more or less enlarged base are practically unknown from most of Mexico. However, they are present in Guatemala and adjacent Chiapas. It seems probable that northern flint corns may be among various cultural traits which spread from south of the

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Isthmus of Tehuantepec into the eastern United States without leaving any very clear record of the route by which they journeyed.

If the northern flints did come from Guatemala, it is still necessary to explain their low knob number, since many of their ear and plant characters are essentially those Mangelsdorf and Cameron ('42) found to be correlated with high knob number in their Guatemalan survey. They interpreted the high knob number as due to crossing with teosinte, which is known to have a very high knob number and which, according to Mangelsdorf and Reeves' hypothesis ('39), was itself derived from previous hybridization between maize and Tripsacum. On these hypotheses, therefore, the high knob numbers and the associated characters came ultimately from Tripsacum, and Mangelsdorf and Cameron applied the term "tripsacoid" to these varieties. Since that time, however, Graner and Addison ('44) have reported that Tripsacum australe of South America, unlike its North American relatives, is lacking in terminal knobs. Assuming that Graner and Addison's observations are typical of the cytological picture in Tripsacum australe, then we are faced with the possibility that introgression of Tripsacum germ-plasm into Zea might have various effects upon knob number, as Cutler ('46) has recently suggested. It is quite possible, therefore, that our results with the northern flints can be harmonized with the hypotheses put forward by Mangelsdorf and his collaborators. Before that can be accomplished, however, we shall need to have a much more detailed understanding than we have at present of the relationships between the northern flints and similar varieties in Central and South America.

#### SUMMARY

1. Though no longer of much commercial importance, the northern flints are of interest to anthropologists as a type of corn once very wide-spread in the eastern United States. They are also worthy of consideration by modern corn-breeders as one of the ancestors of modern United States dent corns.

2. A representative collection of northern flint varieties was grown. Its gross morphology, its pachytene cytology, were systematically investigated. The varieties of flint corn from New York and New England are substantially uniform morphologically, cytologically and archaeologically. Similar varieties are also grown on the Northern Great Plains, but the collection from that area is more variable and includes other types, as it has since prehistoric times.

3. The northeastern flints (those from New York and New England) have slender culms, irregular tillers, well-developed flag leaves, few visible prop-roots, and are of early maturity. Their ears are cylindrical, 8- to 10-rowed, with strong shanks and proportionately large cobs. Their kernels are wide, undented, and not pointed. The tassels are wiry, with no condensation. The central spike bears its spikelets in whorls of two pairs: the pairs 4-ranked and decussately arranged on the spike.

4. The pachytene chromosomes of the northeastern flints show few knobs or none at all, and the knobs, when present, are usually small.

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5. There is abundant archaeological evidence to show that similar varieties of corn were common in eastern North America in prehistoric and protohistoric time. Over wide areas in the eastern states they are the only maize so far obtained in archaeological excavations.

6. The northeastern flints were widely grown commercially in the United States in colonial times and afterward. During the first half of the 19th century they were extensively and repeatedly hybridized with soft dent varieties from the South, giving rise eventually to the typical cylindrical-eared dent varieties of the

United States corn belt.

7. Though the amalgamation of the northeastern flints and the southern dents has proceeded for nearly a century, some of the characteristics of the northern flints are still more or less linked in the germ-plasm of modern United States commercial corns. A cytological survey of 65 inbred lines of dent corn showed chromosome knob numbers of from 2 to 8. The inbreds with the lowest knob numbers (i.e. the most flint-like) were most similar to the flints in their external morphology.

8. The origin of the northeastern flints is briefly discussed. While they are, in general, unlike Mexican maize but show strong resemblances to certain varieties from Guatemala, the problem cannot be seriously approached until more detailed information concerning the morphology and cytology of Central and South American varieties is available.

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### EXPLANATION OF PLATES 1-5

In these plates the lance-shaped object at the left-hand margin is a tracing of the first leaf above the ear. In the photographs of the ears each of the divisions on the scale represents one centimeter.

Plate 1. Stevens' Flint-typical plant, ears, and kernels.

Plate 2. Parker's Flint-typical plant, ears, and kernels.

Plate 3. Dakota White, a variety of the Great Plains having many characteristics of eastern flints.

- Plate 4. Twelve-row Dakota. This type is quite different morphologically from the northeastern flints but similar in many ways to certain varieties of the southwestern states.
- Plate 5. Spanish Popcorn. Representative plant, ears, and kernels. A flint of very early maturity whose morphology suggests relationship to both northeastern and Great Plains varieties.



### Stevens' Flint BROWN & ANDERSON—NORTHERN FLINT CORNS

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1.1

PLATE 2



PARKER'S FLINT BROWN & ANDERSON—NORTHERN FLINT CORNS



PLATE 3



### DAKOTA WHITE BROWN & ANDERSON—NORTHERN FLINT CORNS

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PLATE 4



### Twelve-row Dakota BROWN & ANDERSON—NORTHERN FLINT CORNS



Spanish Popcorn BROWN & ANDERSON—NORTHERN FLINT CORNS

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### EXPLANATION OF PLATE

#### PLATE 6

Photographs of charred maize cobs from Gibraltar Site, Wayne Co., Mich., collected by Dr. Emerson F. Greenman, Museum of Anthropology, University of Michigan, summer 1938. "Owasco" (probably before 1200 A. D.). Note the 8-rowed cobs, the wide alveoli, strongly paired rows, and large shanks. Photograph courtesy of Volney Jones and the Museum of Ethnobotany of the University of Michigan.

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PLATE 6

![](_page_27_Picture_2.jpeg)

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BROWN & ANDERSON-NORTHERN FLINT CORNS

1.

### MYCOCANDIDA RIBOFLAVINA

#### CARROLL W. DODGE

Mycologist to the Missouri Botanical Garden Professor in the Henry Shaw School of Botany of Washington University

The following study is based on culture no. 921, resulting from a long series of selections from stock culture no. 321 in the collection of Anheuser-Busch, Inc., St. Louis. The latter was originally isolated from figs by H. J. Phaff and sent under the name Saccharomyces fragilis ?.1

### Mycocandida riboflavina Dodge, sp. nov.

Pseudomycelium ex cellulis longe ellipsoideis,  $10-11 \times 1.6-2.5 \mu$ , ramis lateralibus 1-2(-4) ad quemque nodum, cellulis 1-3. Colonia parva, cremea vel albida, laevis vel subfoveolata, margine tenui. Colonia rugosa cremea, crateriformis, rugis radiantibus, subelevatis, margine crassiori. Gelatina tarde liquefacta. Glucosa, fructosa, mannosa, sucrosaque fermentatae.

Cells in young cultures variable in shape from ellipsoid to long-ellipsoid, or ovoid, often with both ends rather acute, budding polar, but cells not apiculate as in Kloeckera (Pseudosaccharomyces), mostly single, a few in short chains.

In old liquid cultures (four months) similar to young cultures but chains somewhat longer with 2 (rarely up to 4) short branches at the nodes (up to 3 cells long), cells ellipsoidal to subpyriform, terminal cells short-ellipsoid to nearly spherical; one spherical cell seen with 4 buds at one end and 3 at the other. On old malt agar cultures, pseudomycelium well developed, cells 10–11 imes 1.6–

2.5µ, branching lateral, only 1 or 2 branches at a node, cells long-ellipsoid or with the end bearing the branch slightly enlarged and more rounded; terminal cells shorter.

No ascospores produced on old cultures (some completely dried out) nor on gypsum blocks nor on Gorodkova agar.

#### COLONY CHARACTERS AND SECTORING

On malt extract agar (15° Balling), colony small, margin thin, sloping gently to the center, surface smooth with very minute pitting and with some very shallow radial valleys, with a small rugose sector. Transfers from the rugose sector produced colonies with a shallow central crater, with low broad radial folds and a few cross folds, margin circular and somewhat elevated, with a smooth sector occupying about one-sixth the circle. Colonies cream buff with a lighter margin. Transfers from the smooth sector produced colonies with a very low dome in the central crater, sloping gently to the margin, with 4 or 5 radial valleys, surface smooth with some very shallow pits (visible under a 9  $\times$  hand-lens), margin very smooth and slightly elevated. Colonies cartridge buff or darker, margins somewhat lighter. No further sectoring occurred on smooth colonies.

<sup>1</sup>Mrak, E. M., H. J. Phaff, R. H. Vaughn, and H. N. Hansen. Yeasts occurring in souring figs. Jour. Bact. 44:441-450. 1942.

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